

HYBRIDIZATION BETWEEN *COWANIA MEXICANA* VAR.  
*STANSBURIANA* AND *PURSHIA GLANDULOSA*  
(ROSACEAE)

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ABSTRACT

The hybrid combination *Cowania mexicana* var. *stansburiana* × *Purshia glandulosa* has been observed at two locations in Inyo Co., California. Morphological intermediacy, reduced fertility, and the addition of species-specific flavonoids document hybridization in the narrow altitudinal zone of the species' overlap at these localities. A unique aspect of this study is that leaf flavonoid complements of the two species and hybrids are the same whereas petal flavonoid complements are different subsets of the leaf flavonoid constituents. The discovery of this hybrid documents the third possible hybrid combination among three taxa (including *P. tridentata*) that are currently classified within two genera and magnifies the question of the logic of this classification.

*Cowania mexicana* var. *stansburiana* (Torr.) Jeps. and *Purshia glandulosa* Curran are long-lived shrubs or small trees of the Rosaceae. Within the southern Great Basin, they form a significant component of the vegetation from 850–2700 m (Fig. 1). These two species, with *P. tridentata* (Pursh) DC., have been the subjects of numerous studies because of their conspicuous abundance and importance as range plants. Ecological (Nord, 1965; Mortenson, 1970) and range management studies (USDA, 1937; Plummer et al., 1968; USDA, 1975; Blauer et al., 1975) make up the bulk of the literature.

*Cowania*, with three or four species, and *Purshia*, consisting of two species, have been regarded as well-defined genera because of obvious differences in number of carpels, appearance of fruits, and other divergent morphological characters. In spite of this, several authors have noted interspecific and intergeneric hybridization (Brandeggee, 1903; Stebbins, 1959; Stutz and Thomas, 1963; Nord, 1965; Blauer et al., 1975).

This paper presents morphological, chemical, and fertility data that document hybridization between *Cowania mexicana* var. *stansburiana* and *Purshia glandulosa*. Although this hybrid combination has been suggested as possible and probable (Brandeggee, 1903; Thomas, 1957; Stutz and Thomas, 1963), no documentation of either artificial or natural hybrids exists. The results of this study are of special interest in that they document the third possible hybrid combination among three taxa that are currently classified within two genera.

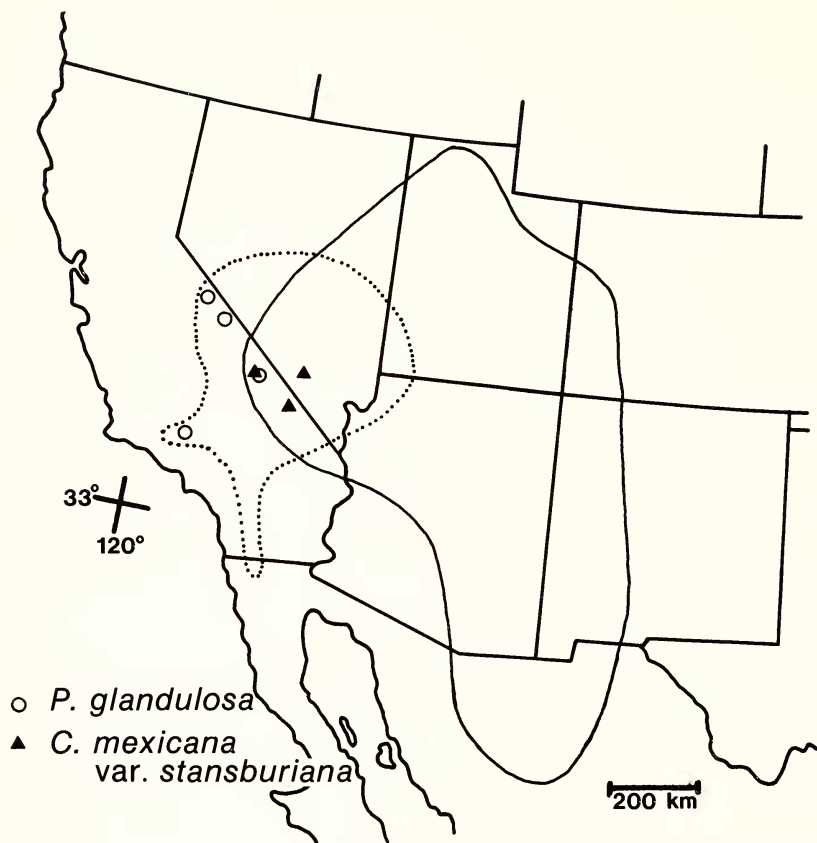


FIG. 1. Geographic distribution of *P. glandulosa* (dotted line) and *C. mexicana* var. *stansburiana* (solid line), and locations of populations used in this study.

Brandege (1903), describing a plant he collected in the Providence Mountains of southeastern California and that he called *Cowania mexicana* var. *dubia*, stated that "this form was also collected by Dr. C. A. Purpus on Morey Peak, Nevada in 1898, and he considered it a hybrid between *Cowania* and *Purshia*." No indication was given by Brandege of which species of *Purshia* Purpus considered to be parental, although a Purpus specimen (6356, UC) is clearly labelled *Cowania Mexicana* × *Purshia glandulosa*. Subsequent collections and observations in the Providence Mountains indicate that *P. glandulosa* and *C. mexicana* var. *stansburiana* are abundant there, but *P. tridentata* does not occur that far south (Munz, 1959). Nord (1965) interpreted Brandege's *C. mexicana* var. *dubia*, from the Providence Mountains, and Purpus' collection from Morey Peak, Nevada, as hy-

brids between *P. tridentata* and *C. mexicana* var. *stansburiana* and proposed the hybrid be called "Purpus cliffrose (*C. mexicana* var. *dubia* Bdg.)".

Stebbins (1959), using his observations and the preliminary data of H. Stutz, P. Plummer, A. Holmgren, W. S. Boyle, and L. K. Thomas, concluded that sympatric hybridization and introgression between *P. tridentata* and *C. mexicana* var. *stansburiana* is widespread. In the same paper, Stebbins (1959) stated that *P. tridentata* and *P. glandulosa* form such extensive hybrid swarms that the identity of the parental types is completely obliterated, although no quantitative data were presented. These putative hybrid swarms occur along the eastern side of the Sierra Nevada and elsewhere in central and eastern California (Koehler, unpubl. data).

Stutz and Thomas (1963) documented that *C. mexicana* var. *stansburiana* and *P. tridentata* frequently form fertile hybrids in nature, ranging from a relatively few putative  $F_1$  hybrids to situations that suggest the presence of  $F_2$  segregates as well as  $F_1$  and backcross derivatives, depending on the slope exposure of parental populations. These authors also suggested that *P. glandulosa* appears to be a stabilized segregate from hybrids of *C. mexicana* var. *stansburiana* and *P. tridentata*.

Artificial hybridization by pollinating emasculated flowers of *C. mexicana* var. *stansburiana* with pollen from *P. tridentata* has produced viable seeds and seedlings (Blauer et al., 1975).

Knobloch (1972) listed 2993 reports of intergeneric hybridization in flowering plants and stated that hindrance of acceptance of hybridization as a potent evolutionary force results from lack of knowledge of the extent of the process in nature. The bulk of literature dealing with homogamic intergeneric hybridization describes crosses that were artificially derived, such as *Helianthus*  $\times$  *Viguiera* (Heiser, 1963), *Lycopersicon*  $\times$  *Solanum* (Rick, 1951, 1960), *Lychnis*  $\times$  *Silene* and *Melandrium*  $\times$  *Silene* (Kruckeberg, 1962), *Hordeum*  $\times$  *Agropyron* (Kruse, 1974), *Tripsacum*  $\times$  *Zea* (Mangelsdorf and Reeves, 1938), and others in the Gramineae (Stebbins, 1950). Observations of natural intergeneric hybridization such as *Cowania*  $\times$  *Purshia* (Stutz and Thomas, 1963) and *Encelia*  $\times$  *Geraea* (Kyhos, 1967) are limited, except in the Orchidaceae where natural hybrids between genera are common (Pijl and Dodson, 1966).

## METHODS

Two mixed stands of *C. mexicana* var. *stansburiana* and *P. glandulosa* containing putative hybrids were observed in the field and specimens were collected for study. Specimens from monotypic stands of each species were also collected for comparison (Fig. 1). The putative hybrids occur on the east flank of Cerro Gordo and Waucoba

TABLE 1. MORPHOLOGICAL COMPARISON OF *Cowania mexicana* VAR. *stansburiana*, *Purshia glandulosa*, AND PUTATIVE HYBRIDS. Numerical values represent the mean of 10 measurements on each of 5 individuals from 4 populations (20 plants) of *P. glandulosa* and of 5 individuals from 3 populations (15 plants) of *C. m.* var. *stansburiana* and of the 14 hybrids. Numbers in parenthesis are the ranges of means of 10 measurements/individual.

Character	<i>C. m.</i>	Hybrids	<i>P. g.</i>
Pistil number	5.0 (4.2-6.4)	2.4 (2.0-3.0)	1.2 (1.0-1.3)
Style length in fruit (cm)	3.8 (3.0-4.3)	1.9 (1.6-2.2)	0.7 (0.6-0.8)
Style pubescence in fruit	plumose	short villous	puberulent
Achene shape	oblong	intermediate	obovate
Achene ratio, L/W	3.6 (3.0-4.3)	2.3 (2.2-2.7)	2.0 (1.9-2.2)
Achene pubescence	villous	villous-hirsute	short pubescent
Hypanthium pubescence	glabrous	spare	tomentulose
Stamen series	2	2 (see text)	1
Number of stamens	>80	52.0 (43-70)	<30
Petal shape	obovate	intermediate	spatulate

Mountain, located respectively near the south and north ends of Saline Valley, Inyo County, California. On Cerro Gordo, *C. mexicana* var. *stansburiana* ranges from 1600 to 2200 m and *P. glandulosa* ranges from 1350 to 1800 m. At Waucoba Mt. the two species range from 1850 to 2100 m and from 1700 to 2000 m, respectively. Hybrids were growing along roads and in washes paralleling roads in a narrow altitudinal zone of species overlap. Fourteen apparent hybrids were found at the two localities. No other mixed stands or hybrids were encountered in these mountains or in other ranges of the region.

A variety of morphological characters distinguish the parental taxa and hybrids. Table 1 shows the most striking and consistent differences. A hybrid-index value for each of the 49 plants studied was derived by assigning the character states given in Table 1 a value of 2 for *Cowania*-like characters and a value of 0 for *Purshia*-like characters; intermediate states were assigned a value of 1. Voucher specimens are deposited at UCSB.

Fertility was estimated from pollen stained for at least 24 hours in 1 percent aniline blue in lactophenol. Five hundred pollen grains were scored from each of 10 specimens of each population. Ten flowers were sampled from each of the 14 putative hybrids. Pollen grains that stained evenly were considered viable; unstained and unevenly stained grains were considered inviable.

Comparison of flavonoids of flowers and leaves was performed by standard techniques (Harborne, 1967, 1968, 1973; Mabry et al., 1970). Twelve flavonoids were identified and individual plants were compared by two-dimensional paper chromatography using identified compounds as markers.

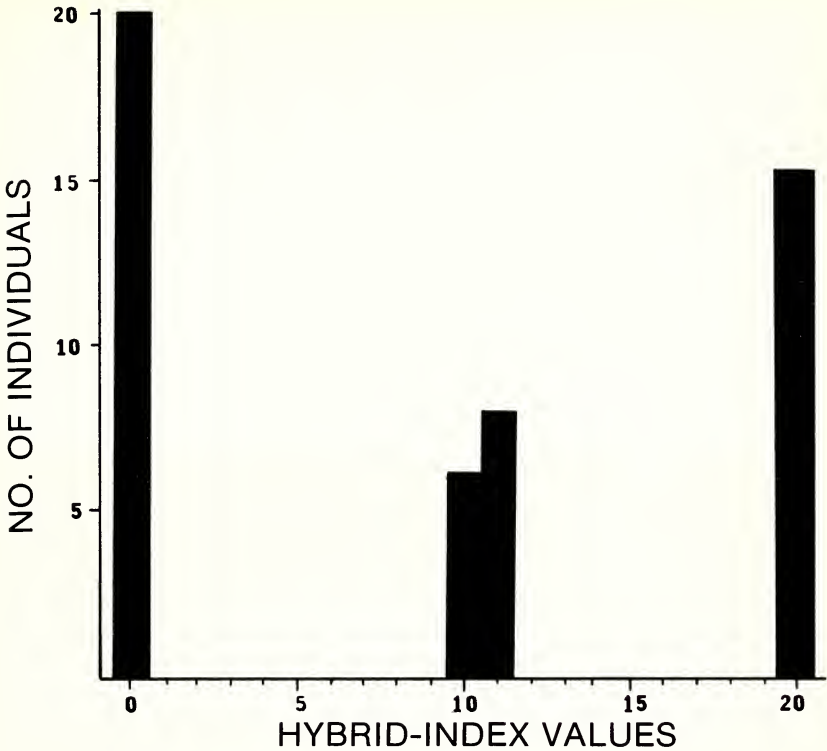


FIG. 2. Histogram of the hybrid-index values for 49 plants. The character states given in Table 1 were assigned a value of 20 for *Cowania*-like characters and a value of 0 for *Purshia*-like characters; intermediate states were assigned a value of 10.

#### RESULTS

*Morphological comparison.* Several floral and mature fruit characteristics distinguish *C. mexicana* var. *stansburiana*, *P. glandulosa*, and the putative hybrids (Table 1; Figs. 2–3). Some contrasting characters and a typical intermediate are shown in Figs. 4 and 5. Vegetative characters such as leaf shape, number of lobes per leaf, leaf margin revolution, and glandularity, as used in earlier studies of hybridization between *P. tridentata* and *C. mexicana* var. *stansburiana* (Thomas, 1957; Stutz and Thomas, 1963), were too variable within and overlapping between populations to be of value. Field identification of individuals in overlapping and contiguous areas was difficult when both flowers and fruits were lacking.

*Pollen stainability.* *Cowania mexicana* var. *stansburiana* averaged 93.4 percent stainable pollen, ranging from 84.0 to 99.0 percent

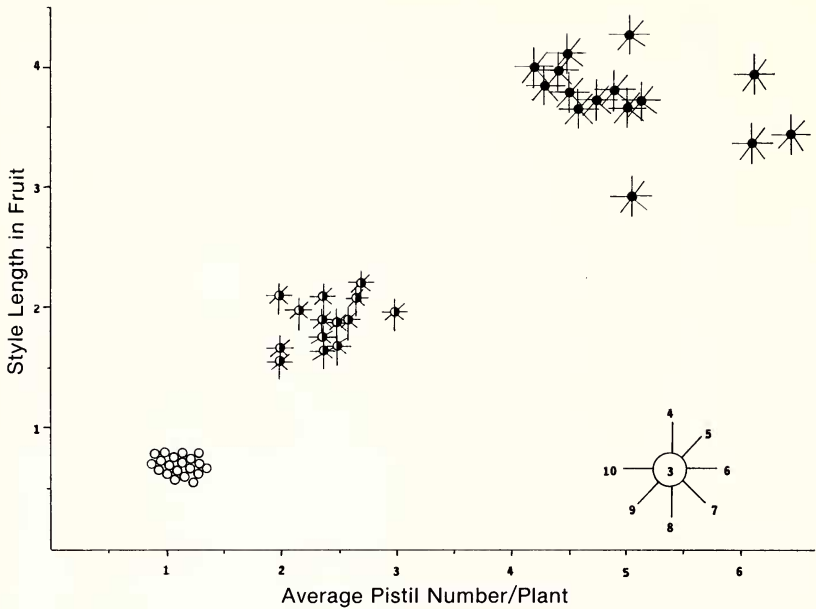


FIG. 3. Scatter diagram for 49 plants. The symbol in the lower right-hand corner indicates the character numbers listed in Table 1. Black circle and full-length glyph indicate *Cowania*-like characters. Open circle and no glyph indicate *Purshia*-like characters. Intermediate characters score as half values.

for all plants sampled from three populations. *Purshia glandulosa* averaged 81.2 percent stainable pollen, ranging from 22.8 to 99.4 percent for all plants sampled from four populations. Stainability of hybrid pollen was comparatively low, averaging 24.4 percent and ranging from 7.8 to 55.8 percent. Six hybrids were higher than the lowest value recorded for *P. glandulosa*, while three individuals of *P. glandulosa* were below the highest value recorded for hybrids. Forty-five percent of *P. glandulosa* individuals had percentages below the lowest value recorded for *C. mexicana* var. *stansburiana*.

*Flavonoid constituents.* Twelve compounds were identified from bulk leaf extracts of *C. mexicana* var. *stansburiana* and *P. glandulosa*. The two species and the hybrids possess the same leaf flavonoids (Fig. 6; Table 2). A corresponding analysis of petals showed that the two species differ significantly (Table 2). Petal extracts of the two species shared five quercetin glycosides. *Purshia glandulosa* petal extracts yielded a rhamnetin 3-O-glycoside not found in petals of *C. mexicana* var. *stansburiana*, while the latter species contained the aglycone quercetin and five glycosides based on the aglycones luteolin, gossypetin and corniculatusin not found in petal extracts of *P. glandu-*

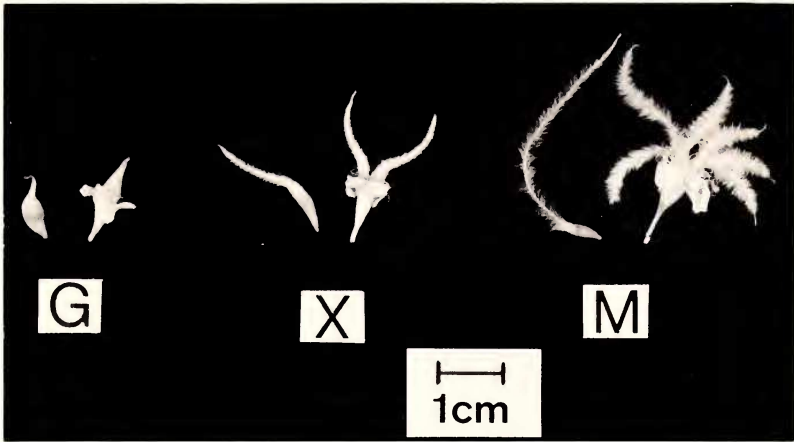


FIG. 4. Fruits of *P. glandulosa* (G), *C. mexicana* var. *stansburiana* (M), and a hybrid (X).

*losa*. Flavonoids extracted from petals of hybrids matched the combined petal flavonoid complements of *P. glandulosa* and *C. mexicana* var. *stansburiana* (Fig. 7). No flavonoids unique to the hybrids were found. Six hybrids lacked sufficient petals to determine their flavonoid complements.

#### DISCUSSION

Hybridization occurred in the overlap zone of populations at two locations, separated by forty miles, in the Inyo Mountains of south-

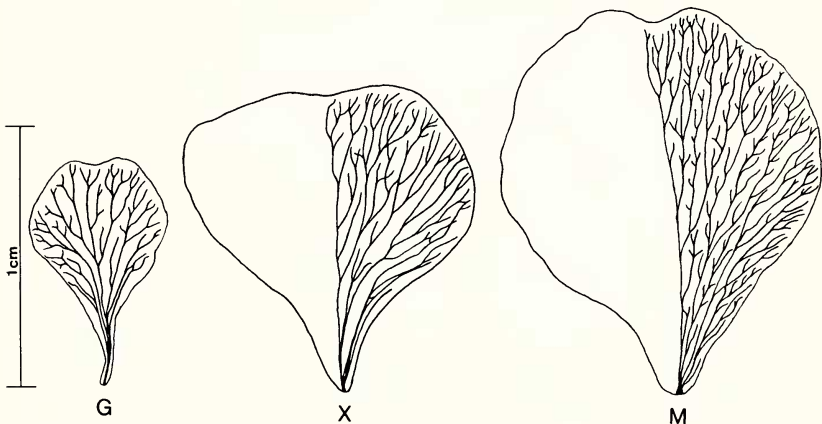


FIG. 5. Drawing of petals of *P. glandulosa* (G), *C. mexicana* var. *stansburiana* (M), and a hybrid (X).

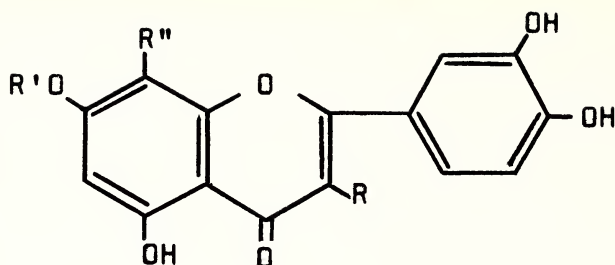


FIG. 6. The compounds isolated in this study were based on the aglycones represented above (LUTEOLIN;  $R = R' = R'' = H$ . QUERCETIN;  $R = OH, R' = R'' = H$ . RHAMNETIN;  $R = OH, R' = CH_3, R'' = H$ . GOSSYPETIN;  $R = R'' = OH, R' = H$ . CORNICULATUSIN;  $R = OH, R' = H, R'' = OCH_3$ ).

eastern California. Hybrids grew in obviously disturbed areas near roadsides. Although the surrounding terrain at both sites is very rugged, broken, and naturally disturbed, several trips to both sites yielded no other obvious hybrids. The onset of flowering in both species is gradual from low to high elevation and the flowers are short-lived. This tends to reduce pollen flow between the species at these sites because *C. mexicana* var. *stansburiana* occurs generally at the higher elevation and *P. glandulosa* at the lower. This is similar to the isolation between *C. mexicana* var. *stansburiana* and *P. tridentata* (Stutz and Thomas, 1963). Pollinator specificity is not known. No sterility because of differences in chromosome number is expected because both species have  $n = 9$  (Baldwin, 1951; Blauer et al., 1975).

TABLE 2. FLAVONOID COMPOUNDS OF PETAL EXTRACTS OF *C. mexicana* var. *stansburiana*, *P. glandulosa*, AND PUTATIVE HYBRIDS. The 12 compounds are all found in and are the major flavonoid constituents of the leaves of the two species and the hybrids.

Compound	<i>Cowania</i>	Hybrids	<i>Purshia</i>
Luteolin 7-0-Glucoside	×	×	
Gossypetin 3-0-Glucogalactoside	×	×	
Corniculatusin 3-0-Glucoside	×	×	
Corniculatusin 3-0-Rutinoside	×	×	
Corniculatusin 3-0-Diglycoside	×	×	
Quercetin (as the free aglycone)	×	×	
Quercetin 3-0-Glucoside	×	×	×
Quercetin 3-0-Galactoside	×	×	×
Quercetin 3-0-Rutinoside	×	×	×
Quercetin 3-0-Glucoxyloside	×	×	×
Quercetin 7-0-Glucoside	×	×	×
Rhamnetin 3-0-Glycoside		×	×



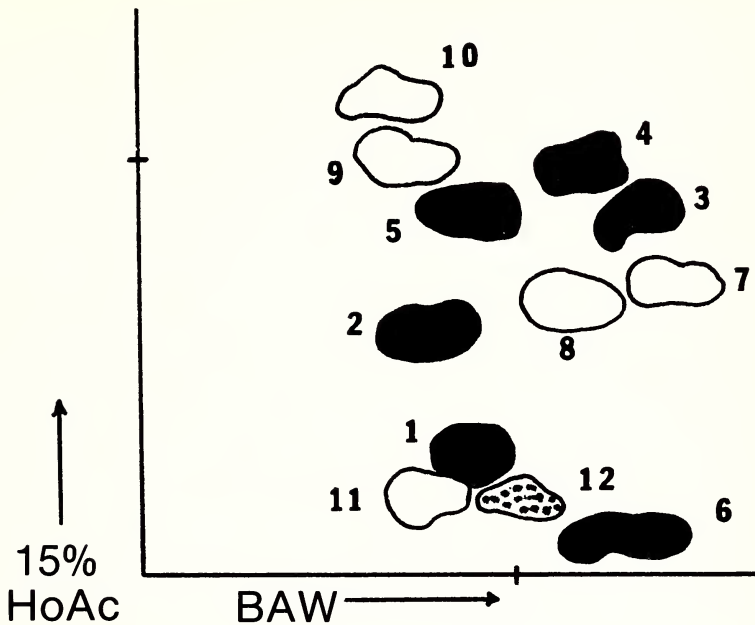


FIG. 7. Diagrammatic representation of the spots revealed on paper chromatograms of the petal extracts of *C. mexicana* var. *stansburiana*  $\times$  *P. glandulosa* hybrids. The unshaded spots are common to both putative parental species, the shaded spots are specific to *C. mexicana* var. *stansburiana*, and the speckled spot is specific to *P. glandulosa*. The numbers refer to the compounds listed in Table 2.  $R_f$  0.50 indicated by cross lines on axes.

No other mixed populations or hybrids were encountered in the Inyo Mountains or other mountains of this region. Mountain ranges to the south and east, such as the Providence and New York Mountains of California, and the Spring and Palmetto Mountains of Nevada, contain numerous populations of each species but mixed stands are rare and no hybrids were observed. Contact between the species is relatively rare and in turn hybridization rare in the mountains near the California-Nevada border.

*Pollen stainability.* Average pollen fertilities of the two parental species is high. Overall fertility of the fourteen hybrids is significantly reduced. The range (7.8–55.8 percent) suggests that the hybrids are varied in their genetic make-up. Pollen fertility of *P. glandulosa* was low compared with *C. mexicana* var. *stansburiana* and *P. tridentata*, which had an average of 94.5 percent and a range of 90.0–97.6 percent (Koehler, unpubl. data). This is consistent with the hypothesis that *P. glandulosa* is a segregation product of *C. mexicana* var. *stansburiana*  $\times$  *P. tridentata* that retains genetic variability. With *P. glandu-*

*losa* retaining heterozygosity one might expect a broad fertility range in  $F_1$  hybrids of *C. mexicana* var. *stansburiana*  $\times$  *P. glandulosa*.

*Morphological comparison.* Morphological data demonstrate the overall intermediacy of hybrids in relation to the parents. Only one character, stamen series, failed to score in a range dissimilar to either species in any of the hybrids. Stamen insertion in hybrids was highly irregular but best characterized as two series. Except for stamen series, the hybrids had a character state distinct from either species for each of the observed characters. Interplant variation in most characters indicated a high degree of morphological variability comparable with that expressed in the broad range of pollen fertility.

*Flavonoid constituents.* Although leaf flavonoid complements of *C. mexicana* var. *stansburiana* and *P. glandulosa* are the same, petal flavonoid complements are distinctive. Therefore, qualitative data showing addition of petal flavonoids in morphologically intermediate plants lends strong support to the theory of their hybrid origin. It has been shown that flavonoid compounds are often inherited as simple dominant characters, involving only one or a few genes (Alston, 1964; Brehm and Ownbey, 1965, 1968; Ownbey and Brehm, 1965), and addition of flavonoids has been observed in many studies of hybridization (e.g., Alston et al., 1962; Alston and Turner, 1963; Smith and Levin, 1963; Crawford, 1974).

A unique aspect of the results is that the sum of the twelve petal flavonoids is found in the leaves of both species. This indicates that both parental species have the same overall genetic complement for the production of flavonoids but that different modifier genes are operative in the production of petal flavonoids. Genes controlling flavonoid synthesis in these taxa apparently fall into three classes: those controlling general production, those modifying chemical structure, and those controlling distribution within the whole plant. The difference in specific petal flavonoid complements is not a relatively simple one such as the production of variants that differ only slightly in structure, but is based on the presence or absence of different compounds that are themselves uncommonly substituted.

These data indicate a close relationship between *C. mexicana* var. *stansburiana* and *P. glandulosa* in their identical leaf flavonoid complements, yet their petal flavonoid complements demonstrate a basic difference that supports morphological and ecological differences. The chemical data also emphasize the importance of studying floral as well as vegetative flavonoids.

*Relationship to previous Cowania-Purshia studies.* Examination of the type specimen of *Cowania mexicana* var. *dubia*, collected by T. S. Brandegee in the Providence Mountains of southeastern California in 1902, and of a specimen Brandegee considered to be of the same variety, collected by C. A. Purpus on Morey Peak, Nevada in 1898, indicates that they are both hybrid plants derived from *P. glan-*

*dulosa* × *C. mexicana* var. *stansburiana*. Both specimens have characteristics ascribed to the hybrids of this study. Several comparisons, such as pollen stainability and flavonoid analysis, could not be made but their morphological characters fall easily into the ranges of hybrids examined in this study. It was considered by one author (Nord, 1965) that these specimens were hybrids between *P. tridentata* and *C. mexicana* var. *stansburiana*. This suggestion can be negated on several points. The Providence Mountains are geographically removed from the southern limit of *P. tridentata* by approximately 268 km, but *P. glandulosa* and *C. mexicana* var. *stansburiana* populations can be found within a few kilometers of each other there. Morey Peak, Nevada, where Purpus collected his specimen, lies within the range of all three taxa. However, the specimen lacks distinctive *P. tridentata* characteristics, is similar to hybrids of this study, and was labelled *Cowania Mexicana* × *Purshia glandulosa* by Purpus, suggesting that it is also a hybrid derived from *C. mexicana* var. *stansburiana* and *P. glandulosa*. It is noteworthy that in 1898 Purpus recognized this plant as an intergeneric hybrid.

There seems little doubt that hybridization occurs between *C. mexicana* var. *stansburiana* and *P. glandulosa*. The data identify a well-established syndrome of hybridity: reduced fertility, morphological intermediacy, and the addition of species-specific flavonoids. The range of pollen fertility was suggestive of hybridization beyond the first filial generation, but petal flavonoid complements of eight hybrid individuals are the exact summation of parental complements. These eight individuals had pollen fertility averages below 21 percent and were the lowest of the 14 discovered hybrids in this regard. If these plants were the result of backcrossing, selfing, or intercrossing of F<sub>1</sub> hybrids, the effects of segregation on the flavonoid constituents would be expected in the petal flavonoid complements.

This documentation of hybridization between *C. mexicana* var. *stansburiana* and *P. glandulosa* closes the ring of possible hybrid combinations in this three-taxon complex and magnifies the question of the logic of the current classification. The occurrence of hybridization among the three taxa allows a strong case for merging the taxa into one genus. The data of this study and others (Thomas, 1957; Stebbins, 1959; Stutz and Thomas, 1963; Blauer et al., 1975) indicate a close genetic relationship that is clouded by seemingly major differences in carpel characters. However, without comprehensive study that includes the other taxa of *Cowania*, submerging taxa that long have been considered distinct and are important range plants would be premature.

#### ACKNOWLEDGMENTS

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#### ANNOUNCEMENT

##### PAPERS IN WESTERN PLANT ECOLOGY HONORING JACK MAJOR

A symposium to honor Dr. Jack Major on the occasion of his retirement will be held at the University of California, Davis, on Friday, 29 May 1981, 9 a.m. to 5 p.m. Twelve to 13 papers will be presented, each 25 minutes long.

People wishing to contribute papers are invited to submit abstracts to Dr. Michael Barbour before 15 February.

The symposium will be co-sponsored by the California Botanical Society; the Botany Department, UC Davis; and UC Davis Institute of Ecology. The proceedings will be published in the Institute of Ecology series. Admission will be free.

An honorary dinner will be held from 7–9 p.m.

For further information and dinner reservations, call or write: DR. MICHAEL BARBOUR, Botany Department, UC Davis 95616: (916) 752-2956.